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OBSERVATIONS ON THE SWARMING FLIGHT AND MATING OF *CULICOIDES* (DIPTERA: CERATOPOGONIDAE).[1]

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1. Introduction.

Observations and experiments on certain aspects of the sexual behaviour of the blood-sucking midges, *Culicoides* spp., have been made, as opportunities occurred, over a period of several years. This report is a record and a discussion of the information collected, which, though it is obviously incomplete and in some respects fragmentary, nevertheless leads to a number of interesting generalisations and conclusions.

These midges, like many other Nematocera, often gather in discrete "dancing swarms" consisting largely of males. It is commonly assumed, perhaps more

[1] Contribution No. 3240, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada. Most of the observations on which this paper is based were made while the author was on the staff of the University of Glasgow. A few of the observations and much of the discussion result from work done in the employ of the Entomology Division, Ottawa.

often than it is demonstrated, that such swarms of flies have a sexual function. The male swarms of *Culicoides* spp. were examined in an attempt to discover, first, the causes (stimuli and responses) leading to their formation; secondly, the way in which the details of the flight pattern of the swarming insects are controlled; and thirdly, their possible function as mating swarms and how mating ultimately takes place. The ability of certain species to mate without swarming was also investigated. The plan of the paper is to deal first with each species separately, recording the observations and making certain comments, and then to summarise the whole in the discussion.

In a preliminary note (1950) the writer briefly indicated that the male swarms of *Culicoides nubeculosus* (Meigen) always formed over conspicuous objects, the "swarm-markers". It was suggested that the position of the swarm was determined by a visual response to the marker, and that each individual responded separately; the swarm therefore was a mere group of insects each attracted by the marker, rather than an organised unit. The constant upwind orientation of the midges in the swarm suggested that movement-vision was involved in the response, since a stationary marker as seen by an insect flying in moving air would appear to be moving upwind (see p. 229). The occurrence of mating in the swarm was demonstrated; and it was suggested that the males perceived the presence of a female among them by means of their antennae, which would function as auditory organs, sensitive to the sound of a flying female, when the long antennal setae were erected. Mating between non-flying males and females, without sound production or auditory response, was also recorded. In this paper these and related matters are considered in greater detail, and also in relation to other species of *Culicoides* and certain other Ceratopogonidae.

Pomerantzev (1932) had already shown that mating occurred between non-flying individuals of *C. nubeculosus*. His valuable paper also gives an account of the structure and function of the reproductive organs of both sexes, including figures of the positions of the parts during copulation. Goetghebuer (1919, 1920) recorded the occurrence of male swarms in certain species. These apart, little has been written on the matter.

Parker (1949) showed that a number of species of *Culicoides* have more or less specific times of flight; and that there may even be differences in the time of flight of the male and female of the one species. The method he used was not, however, adequate for distinguishing the swarming flight from flight of a more general nature. Downes (1950) indicated that in *C. nubeculosus* there are in fact definite times of swarming. In the present studies little attention was given to these aspects, which are not related immediately to the cause and function of the swarms but merely define the conditions of time of day, light intensity, etc., at which swarming takes place. Most observations, however, were made in the evening, from before sunset until near darkness, and it is clear that for many species this includes the habitual swarming period, as well as that for general flight.

All the more extended observations were made at Chideock, Dorset, and at Airth, Stirlingshire. The Chideock site is a farmyard, and *C. nubeculosus*, typical of the habitat, breeds in very large numbers in puddles and marshy areas heavily contaminated by the excreta of cattle. A roadway of light-

coloured sand and gravel runs through the farmyard and all observations on swarms were made along this road. Some ten other species of *Culicoides* are found more or less abundantly in the same farmyard.

The site at Airth, near the south end of Kincardine Bridge, consists of a small area (about 50 yd. square) of low-lying pasture, separated by an embankment from the salt marshes which there form a wide expanse along the Firth of Forth. The area is watered mainly by drainage from higher pasture inland, but is occasionally flooded by spring tides pouring through a channel in the embankment. This happens so seldom, however, that it has little effect on the vegetation. The site contains a small pool, often visited by cattle, which is surrounded according to the season by a varying expanse of bare and dark muddy ground ; beyond this, grass grows in hummocks separated by channels of similar bare and dark mud, which become less numerous and narrower as the higher pasture is approached.

This marsh is an extremely interesting area in which both salt-marsh and inland species are found. Three salt-marsh species (*C. riethi* Kieffer, *C. circumscriptus* Kieffer var. (?) and *C. halophilus* Kieffer) and three inland forms (*C. nubeculosus*, *C. stigma* (Meigen) and *C. odibilis* Austen) were reared from a single sample of mud ; and *C. maritimus* Kieffer (salt-marsh) and *C. pulicaris* (L.), *C. punctatus* (Meigen) and *C. chiopterus* (Meigen) (inland) were taken in flight and may well breed there also. On the salt-marsh the four coastal species occur in greater numbers, mixed with only small numbers of the others, which alone are found on the higher parts of the pasture. The occurrence together of *C. nubeculosus* and *C. riethi*, hitherto considered as restricted respectively to farmyards, sewage beds, etc., and to salt marshes, is noteworthy.

2. *Culicoides nubeculosus* (Meigen).

(a) *The Male Swarms : Characteristics, Cause and Function.*

Most of the following observations were made on the sandy roadway at Chideock between 10th and 29th July, 1948 ; swarming, however, took place on only seven of these days, for, as with other species of the genus, the flight of *C. nubeculosus* is inhibited by any but the slightest wind.

The first two swarms were discovered on 10th July and consisted of about 20 and 50 individuals respectively. About half of each was captured and all specimens were males of *C. nubeculosus*. The swarms were located above wet areas, each some 2 ft. square, on the surface of the road ; the local wetting had produced a mud that was much darker than the general light sandy-brown colour. They remained above these dark wet patches for the whole hour of observation, and re-formed rapidly whenever they were disturbed, e.g., by netting part of the group. They were roughly columnar in shape and commonly extended from 2 ft. or 3 ft. to 8 ft. above the ground and averaged about 1 ft. in diameter. The insects in the swarms were engaged in constant side-to-side flight with a traverse of 6 in. to 12 in., and less frequently made forward-and-backward or vertical excursions, but all facing in the one direction and retaining the same orientation throughout the evolutions.

On later dates, swarms ranged from 1 to about 70 individuals. They consisted of males of *C. nubeculosus* only, except for one record of a single female

(200 specimens examined from 11 swarms). Swarming was usually in progress when observations started at about 19.30 hr. G.M.T., although on one clear hot evening it did not begin until 20.15 hr.; and it continued at least until it was too dark to observe, about 20.40 hr.–21.00 hr. The swarms were found not only above the dark wet areas but also, and more frequently, above fresh (wet) and old (dry) pads of cow-dung, both of which were likewise much darker than the road surface. The normal position was always directly above such an object —the swarm-marker.

Though no exact measurements were made it was clear that both the size and height of the swarm varied with the size of the swarm-marker. Those over pads of cow-dung were little more than 1 ft. above the surface and consisted of a dozen or so individuals, whereas those over patches of dark mud several square feet in area averaged 30 to 50 insects and the base of the swarm was at a height of 2 ft. to 4 ft. and the column extended upwards to about 8 ft. These larger swarms tended to fluctuate in height, and occasionally the whole swarm rose, apparently as one unit, to 12 ft. or more, above which height it could no longer be seen; a few minutes later the swarm reappeared and descended to the normal height.

In the eleven swarms sampled, and in all others observed subsequently, the insects were all oriented in the one direction, and always so as to face the slight breeze. The orientation could be associated with no other factor than wind direction; it might be along or across the road or in an intermediate position and towards or away from the lighter part of the sky. For example, on 13th July there was a slight westerly wind, and the swarms were oriented westward and towards the sunset, and on 21st July, when the wind was from the east, the swarms faced eastward and away from the bright western horizon. In momentary gusts of stronger wind the swarms were carried horizontally a few feet or a few yards downwind, but they regained position directly above the swarm-marker as the gust died away. In persistent stronger winds—above an estimated 2 to 3 m.p.h.—no swarming or other flight occurred.

It seemed possible that the position of the swarm might be determined either visually by the dark colour of the swarm-marker contrasting with the paler road (this feature was common to all the natural swarm-markers) or by a chemical stimulus from the wet mud or the cow-dung. Visual control seemed the more likely, first because old and dried-out cowpads were as effective as fresh ones in producing swarms, and secondly because in a steady breeze, which would carry chemical emanations somewhat downwind, the swarms were nevertheless directly above the marker even to a height of 8 ft.

To test this, an attempt was made to induce swarming experimentally. First, six dark wet areas, each 2 ft. by 1 ft., were made by dampening the surface of the road with stream water. Typical swarms (from a few to 30 individuals) quickly developed over five of these patches. Three dark blue-black cloths, one impregnated with cow-dung, another with water, and the third dry, were then laid on the road: swarms developed over all three. The dry cloth, 3 ft. by 3 ft. in area and larger than any of the natural swarm-markers, was tested in five positions, and in four of them swarms of about 100 individuals, extending from 3 ft. to 10 ft. in height, were produced. The swarm dispersed when a white cloth was spread over the swarm-marker, but usually formed

again when it was removed. All these observations suggest that the position of the swarm is determined visually by the midges' response to a small dark object on a lighter background (Plate I, fig. 1).

Usually, when a swarm-marker was laid down the midges soon began to arrive and often the swarm was well developed within 5 to 10 minutes. The first to arrive immediately took up the characteristic position over the cloth and commenced the typical pattern of flight; and if midges were scarce it might continue alone for a considerable period. Similarly, single specimens were occasionally seen over cowpads. Thus one insect may constitute a swarm, or at least exhibit the behaviour characteristic of each individual of a fully developed swarm. To this extent, therefore, the swarm is not a unit held in being by an internal organisation but is merely a group of insects undertaking the same activity at the same time and place, and responding individually to the same relatively local and rare external stimuli. It is, of course, possible that in the fully developed swarm the insects may exhibit gregarious behaviour due to mutual stimuli and responses, over and above this basic independence. The apparent coherence when the swarm rose suddenly to a higher than normal position is, however, the only observation that cannot readily be interpreted by the simpler hypothesis.

Both natural and induced swarms were watched carefully to discover whether mating was taking place. The observation was difficult because small predaceous flies sometimes entered the swarm and captured one of the insects, thus suggesting a pairing, and also because a small species of chironomid was swarming over the same markers and was mating rather frequently. Nevertheless, six probable pairings of *C. nubeculosus* were seen in two hours; but as the pairs fell towards the ground they passed from a background of bright sky to one of vegetation and were lost to sight. Later, a large white sheet was placed downwind of the marker, where mating pairs drifting out of the swarm would probably fall. The sheet was exposed to swarms of about 50 males on two evenings, for a period of about three hours in all, and two mating pairs of *C. nubeculosus* were collected, one on each evening at about 20.20 hr. The pairs were standing motionless on the sheet, the male and female facing in opposite directions—evidently, therefore, the tip of the abdomen of the male was inverted, since the ventral surface has to be brought into contact with the ventral surface of the female—and in each case they separated within two minutes of being found.

It seems clear that the swarms function as mating swarms; that the females entering them are almost immediately recognised by the males; and that pairing, or at least holding and clasping, begins in flight in the swarm and is completed as the pair drift towards the ground.

When a male was taken from a swarm, the long setae of the antennal flagellum were found in the "erect" position—that is to say, at an angle of about 70° to the shaft of the antenna (samples of eight swarms inspected). Within one or two minutes of capture the setae were gradually folded down until they formed a single pencil lying along the shaft (decumbent position). The latter position is found in all specimens observed in captivity, whether newly emerged or old, reared or captured. It is probable that males with the antennal hairs erected are in the receptive state, able to perceive the sounds

emitted by flying females and so to recognise them as they enter the swarm (Plate I, figs. 2 and 3).

In August and September, 1952, *C. nubeculosus* was also found at Airth, flying in the same area as the much more numerous, and closely related, *C. riethi*. The Airth and Chideock populations, some 450 miles apart, are not necessarily racially identical, though both are clearly *C. nubeculosus* (Meigen) as understood by Edwards (1939). To avoid possible confusion of *C. nubeculosus* and *C. riethi*, all the swarms studied at Airth were sampled ; seven of them were identified as *C. nubeculosus*.

These swarms were small, of 1 to 10 insects only, and were induced experimentally over dry cloths, no natural swarms being discovered. In agreement with the Chideock results, all were of males of *C. nubeculosus* (19 specimens inspected in 7 samples) and the orientation was consistently upwind, but during flight the forward-and-backward and vertical excursions were more frequent and the side-to-side ones less pronounced. The antennal setae, erect during swarming, were folded on capture and not re-erected in the laboratory. Similarly, reared specimens never erected the setae in captivity. In spite of the small numbers, two pairings were seen in the swarms and the pairs behaved as already described.

But although each of the swarms was induced by a marker, two very different types of markers were used. Two swarms formed over small (1 ft. square) black areas on a white field—similar to the Chideock swarms—and one at the downwind margin of a large black sheet ; four others, however, were controlled by white markers on black sheets or dark herbage, two being above the middle of the marker and two above or just in front of the downwind margin. The only common feature here was that the swarm-marker was clearly distinguishable from its surroundings ; there seemed to be no regularity in the choice of light or dark, centre or downwind margin. Nothing similar was met with in any other series of observations.

(b) *The Mating of Non-flying Individuals.*

As already briefly reported (Downes, 1950), *C. nubeculosus* is also able to mate when enclosed in 3 in. × 1 in. glass vials. Under these conditions the insects do not fly, nor are the antennal hairs of the males ever erected, so that both production and reception of sound seem to be excluded. Furthermore, males (with decumbent antennal hairs) will mate with females engaged in feeding and therefore completely immobile and passive. Matings of both types were observed repeatedly and have been used in maintaining a colony over a period of years.

When insects of the two sexes are enclosed in a vial, they make no movement suggestive of recognition as they approach one another, and even when they actually touch during their wanderings the slight contact elicits merely a change of direction. If, however, a male chances to crawl over a female, or if the two are brought together in extensive contact as in the case of one falling off the upright glass wall and upon another on the floor, sexual recognition often occurs. The male then grapples the female with his legs, and, some sort of a hold being eventually obtained, he bends his abdomen, the claspers held widely open, in an attempt to bring the terminalia from below and from behind into contact

with the region of the female opening. When this is achieved and the abdomen of the female is firmly held by the claspers and presumably the aedeagus is inserted into the vagina, the female, which up to now has been struggling, becomes quiescent and remains so until mating ends. The male also usually releases the hold with his legs and stands quiescent on the substrate, facing in the opposite direction. As in the case of mating in flight described above, it is obvious that the terminal segments of the male are now completely inverted. The male of *C. nubeculosus* is remarkable in that the hypopygium (segments 9 and 10) is already more or less inverted even before mating. All degrees of twist from 0°–180° are encountered among wild-caught specimens, with twists of 90°–150° in the majority. On emergence the terminalia are in the normal position, but reared specimens up to two days old show twists of up to 90° ; it seems therefore that twisting takes place gradually during the first few days of adult life. Whether the completion of twisting to 180°—the situation during mating—takes place by muscular action while the male is attempting to grasp the female, or whether it is a mechanical result of the stance taken after mating has been achieved, is unknown. A twist of about 45° occurs between segments 7 and 8, and a somewhat greater one develops between segments 8 and 9. Twisting may take place in either direction.

Occasionally, mating is achieved almost instantaneously after the initial grasping with the legs. Typically, however, the female attempts to escape, and even if already feeding, starts to struggle, so that the claspers of the male seize a leg or some other part of the body. Sometimes mating is achieved after efforts lasting a minute or more ; but rather frequently the pair eventually break apart without having copulated. Nevertheless, the actions signifying sexual recognition are clear enough : the grappling with the legs, the bending of the abdomen and the opening of the claspers. In the small vials in which the experiments were made, both mating attempts and completed matings were very frequent ; on occasion a single male mated seven times in little more than half an hour. Mating usually lasted about 2 to 3 minutes, rarely longer than 6 minutes, and inspection of the spermatheca of the female showed that the matings resulted in impregnation.

It is a remarkable fact that similar sexual recognitions take place not only between male and female but also between male and male, and this suggested investigating the behaviour of males of *nubeculosus* in the presence of females of other species. A series of pairs were set up in 3 in. × 1 in. vials and watched for periods of about 30 minutes. The encounters were classified as *slight* (touching while walking) or *extensive* (insects crawling over one another or falling together), and the resulting behaviour as *no recognition*, *recognition* (grappling but encounter broken off without mating) or *completed mating*. The observations are summarised in Table I.

It appears from these figures that, though slight contacts did not lead to sexual recognition even when the other member of the pair was a female of the same species, the more extensive contacts usually resulted in recognition whether the male was with the appropriate female, another male of the same species, a female of *C. riethi* or a female of *C. halophilus* ; and, so far as the rather small figures allow a conclusion, the male of *nubeculosus* did not distinguish between these four situations. The sensory stimulus that initiates

recognition appears to originate from *Culicoides* rather than from the one sex or the one species.

TABLE I.—*Behaviour of male* C. nubeculosus *with various partners (in small container, flight impossible).*

Partner	♀ *nubeculosus.*		♂ *nubeculosus.*		♀ *rietbi.*		♀ *halophilus.*	
Encounter	Slight.	Extensive.	Slight.	Extensive.	Slight.	Extensive.	Slight.	Extensive.
No recognition .	7	3	7	1	7	0	13	3
Recognition .	0	5	0	8	0	4	0	9
Completed mating	0	3	0	—	0	3	0	(1)

The final results are not, however, identical in all cases. With females of *nubeculosus*, a considerable proportion of the recognition struggles resulted in a completed mating and quiescence. With another male, the shape of the hypopygium itself precludes the taking up of the full mating position, though long struggles ensued in the attempt to clasp the tip of the abdomen. With females of *rietbi*, matings that appeared completely normal were achieved, sometimes very quickly and with little or no struggle; the genitalia of the pair, so far as could be seen externally, locked together in the normal way, the female became quiescent and mating was completed in 5 to 8 minutes. In another experiment it was found that males of *nubeculosus* also recognised and mated with the immobile feeding females of *rietbi*, as they do with those of their own species. *C. nubeculosus* and *C. rietbi* are, of course, closely related, though easily distinguishable by features involving the wings, the thoracic pattern and the genitalia of both male and female. Usually they occur in distinct habitats, but where, as at Airth, the adults fly together and both species can be reared from the same sample of mud, no individuals suggesting natural hybridisation were found. With females of *halophilus* the case is rather different. The numerous recognitions led to exceptionally protracted struggles, but in the one instance (Table I) in which the male eventually seized the tip of the abdomen the grip with the claspers was somewhat askew and the female did not become fully quiescent. These two species belong to very different sections of the genus, and, moreover, *halophilus* is much smaller than *nubeculosus*.

It seems, therefore, that *C. nubeculosus* can mate in two distinct ways. In one, the males collect in small flying swarms over visually recognised objects, meantime holding the antennal hairs in the erect (sound-receptive) condition. From time to time, a female, either by accident or guided by some stimulus, flies into the swarm, where she is recognised auditorily by the male. As the pair come together they drift out of the swarm and copulation is achieved by the time they reach the ground. In the other, males with decumbent antennal hairs recognise crawling or feeding females when they come into extensive contact with them by chance. It must be supposed that tactile sensilla or contact chemoreceptors mediate this recognition; certainly sound production and reception play no part in it. In matings of this type the sensory process involved does not enable the male to distinguish the female of *nubeculosus* from those of certain other species or from another male.

The mating of males of *C. nubeculosus* with feeding females of the same species was first reported by Pomerantzev (1932) in Russia. Observing females attacking cows, he found that a considerable number of males (of *C. nubeculosus* only, although females of four other species attacked the same cows in numbers) also landed. These males found and mated with the feeding females. Records of males of biting Nematocera being attracted to the host of the female are extremely rare. It may therefore be worth recording that once at Chideock a single male of *C. nubeculosus* landed on the author. This is not such a decisive observation as Pomerantzev's, since the Chideock strain of *C. nubeculosus* does not bite man in nature (it will do so readily in captivity ; the natural food is unknown) ; nevertheless, it is the only occasion on which such a landing of a male individual of any species of *Culicoides* has been observed.

3. *Culicoides riethi* Kieffer.

This species is very numerous at Airth, and many swarms, of 1 to about 100 individuals, have been observed. Swarming took place between 15.00 and 19.00 hr. (late August and early September, 1952), and the swarming period overlapped slightly with that of *C. nubeculosus*, which began about 18.00 hr. at the Airth site. The larger swarms were somewhat columnar, from 2 ft. to 3 ft. high and 1 ft. in diameter. The height of flight varied, but usually the base of the swarm was 2 ft. to 4 ft. above the ground.

Natural swarms were noted three times over dry, somewhat bleached cow-dung lying on dark mud and sparse grass ; twice over stones also lighter than the muddy background ; and once above a single upstanding grass hummock surrounded by bare black soil. The common factor appeared to be an area, flat or raised, lighter in colour than the surroundings. By reproducing this situation with white cloths laid either on the mud or on grassy areas or on larger black cloths, swarms were repeatedly induced. With markers smaller than 1 ft. square the swarm appeared to be slightly downwind of the marker, above the downwind margin, or above the middle ; with larger markers (3 ft. square and larger) the swarm was centred approximately over the downwind margin. Probably the exact position with relation to this margin varied with wind strength.

Observation of midges joining the swarm showed that they flew upwind until the first (downwind) margin of the marker was reached. Forward flight stopped approximately above the margin and a short backward movement occurred. Thus the typical swarming dance over the marker began. Backward-and-forward, side-to-side, and up-and-down movements were of similar extent and frequency ; and the side-to-side movements appeared to be regulated by the lateral margins of the marker, since at least over small markers the excursions ended at about the same distance, horizontally, from either margin. The insects faced upwind in all phases of flight as in *C. nubeculosus* ; whenever the wind veered the orientation of the swarm swung with the wind. On another occasion a swarm was watched as the wind strengthened to an estimated 2 m.p.h. With the rising wind the swarm flew lower, from a base height of 2 ft. it fell first to 1 ft. and then to a few inches above the sheet ; finally the insects settled on the sheet, the antennal hairs erect, to take off again when opportunity offered.

The antennal hairs of males netted from a swarm were always erect, but within 2 minutes were folded to the decumbent position. When captured insects were kept in vials re-erection occurred from time to time for several days, but with no apparent regularity. The stimulus leading to erection is unknown. The immediate cause is most probably an increase of fluid pressure in the antennal shaft altering the shape of the cuticle of the flagellar segments so that the articulations bear differently on the setal bases. At all events, if the third (first flagellar) segment of the living insect is squeezed, the hairs of all segments are erected, as they are also if a preserved specimen is soaked in a material, such as concentrated phenol, which causes the body to become turgid (similarly in *C. nubeculosus* and many other species).

The *C. riethi* swarm consists almost entirely of males (191 males, 2 females, in samples of five natural and seven induced swarms) and always of this species only (but see below). It was possible, with this species, to observe that pairing takes place in flight in the swarm; the pairs were seen to come together and then to fall to the ground slightly downwind of the swarm and take up the same position as *C. nubeculosus*. One such mating was completed in 2 minutes. Three mating pairs were examined and in each case both partners were *C. riethi*. Two of the females were dissected and, rather surprisingly, the eggs of both were fully developed and ready for laying.

C. riethi is by no means the only insect on the Airth ground that uses light patches as swarm-markers. Chironomid swarms were often seen, but they were always distinct from those of *C. riethi*; for example, on one occasion there was a small chironomid swarming at 1 ft. above the marker, *C. riethi* was vertically above it at 4 ft. to 5 ft., while at 10 ft. to 14 ft. there was another much larger chironomid. Yet more interesting, once while *C. riethi* was swarming at 4 ft. to 5 ft. over the downwind margin of a 3 ft. $\times$ 3 ft. white sheet, another swarm flying below it at 2 ft. was found to consist of *C. punctatus*. Samples taken at 4 ft. yielded *C. riethi* only; two samples at the 2 ft. level yielded 13 males and 1 female of *C. punctatus* + 1 male of *C. riethi* and 7 males of *C. punctatus* + 1 female of *C. riethi* respectively. Evidently a few low-flying specimens of *riethi* flew at the *punctatus* level; the two swarms, however, appeared distinct both spatially and in rate and pattern of flight. It will be remembered that the local form of *C. nubeculosus* also uses the white marker sometimes; but owing perhaps to the scarcity of this species or to its habit of swarming later in the evening, the two were not seen simultaneously above one marker and no comparison can be made.

In *C. riethi* sexual behaviour can also be initiated by contact under conditions in which flight is impossible and the antennal setae of the male are decumbent. In sharp contrast to *C. nubeculosus*, however, the phenomenon is very uncommon and only three instances were seen: one recognition of a female, one of a male and one completed mating with a blood-sucking female. In spite of the great difference in frequency, therefore, the basic capacities of the two species appear to be very similar.

4. Other *Culicoides* Species.

C. halophilus Kieffer.—Many dozens of swarms of *C. halophilus* were seen at Airth in late August and early September, 1952, usually between

17.00 and 20.00 hr. All were small (2 to 20 individuals) and subspherical, and typically formed very low down, some 6 in. to 10 in. above the ground level over the narrow dark muddy channels (4 in. to 12 in. wide) between grass hummocks. Though both swarms and markers were very numerous, the intervening hummocks probably prevented the low-flying insects from seeing other nearby markers, and the swarms were stable. One swarm over a larger (2 ft. square) mud patch was flying conspicuously higher, at about 2 ft. A number of swarms were induced by laying 1 ft. square black cloths on the grass in the flight area.

Forty-eight specimens from five natural and four induced swarms were all males of *C. halophilus*. *C. nubeculosus*, of course, often uses similar dark markers, but it may be that the small narrow patches that serve for the low-flying *C. halophilus* are too small for a species flying at 3 ft. and higher. In all the swarms inspected the insects were, as usual, facing the wind ; the flight pattern included forward-and-backward and side-to-side movements, but vertical excursions were less conspicuous. As in the other species, the antennal hairs of insects inspected as soon as possible after capture were erect—except in one sample of 5—but folding gradually occurred. Kept in the laboratory in vials, a few individuals were noted with the antennae erect (re-erected?) two days after capture. The genitalia were never twisted ; at most a slight tilt amounting to not more than 15° was sometimes observed.

C. punctatus (Meigen), *C. delta* Edwards, and *C. pulicaris* (L.).—A single swarm of *C. punctatus* was observed at the Airth site. It was induced (25th August, 1952, 19.00–19.30 hr.) over the downwind edge of a white sheet laid on a grass and mud area, and flew at about 2 ft. above the ground. The sheet was being used for studying *C. riethi* and, as already described, a swarm of that species was flying simultaneously though at a greater height above the marker. Two samples yielded a total of 20 males and 1 female of *punctatus*. As usual, all individuals faced upwind and all those in the samples had erect antennal hairs soon after capture.

In May, 1948, swarms of *C. punctatus* (3 males in sample) and of *C. delta* (10 males) were observed on Bannachra Moor, Dunbartonshire. When first seen both swarms were about 10 ft. above the ground, but the swarm of *C. delta* moved much higher on being disturbed. A few days later, in the grounds of Glasgow University, two swarms of *C. pulicaris* were found (10 males and 16 males in samples).

These three species and *C. halophilus* are very closely related forms belonging to the *pulicaris* complex (Downes and Kettle, 1952). It is interesting, therefore, that each of the swarms sampled consisted of one species only, though several others of the complex were flying on the same ground at the time when the various observations were made. Thus, at Airth there were *C. halophilus* and *C. punctatus* ; at Bannachra, *C. delta*, *C. pulicaris* and *C. punctatus* ; and at Glasgow University, *C. pulicaris* and *C. punctatus*.

C. impunctatus Goetghebuer—Four or five pairs of *C. impunctatus* were seen falling through the air and landing on a road beside Little Loch Broom, Wester Ross, on 8th August, 1945, 17.30 hr. Evidently this species mates in flight, and presumably while swarming, since a number of pairs were observed

within a few feet of each other ; the swarm, however, was not looked for, but may have been fairly high.

C. grisescens Edwards.—Several swarms of up to 100 individuals were seen at Auchterawe, Inverness-shire, on 18th September, 1946, 18.30 hr., and another very large one, estimated at several thousands, at the same place on 12th September, 1948, 19.00 hr. In each case the insects were conspicuously oriented upwind. The large swarm was flying at 6 ft. to 12 ft. over the middle of an expanse of very even short grass some 10 yd. in diameter ; there was no discoverable marker underneath it, but it is possible that the swarm was sited so as to be equidistant from the edge of the woodland surrounding the clearing. Samples of three swarms yielded 37, 3 and 67 males of *C. grisescens*, together with several females of other species (the latter probably engaged in hunting the observer).

C. obsoletus group.—A mating pair of *C. obsoletus* (Mg.) was netted at about 3 ft. above ground level on the evening of 29th August, 1946, at Inverness ; this at least suggests that mating occurs in flight. There are no observations on male swarms.

At Chideock, on 7th July, 1949, 17.30 hr., an immense number of females of this group were seen in a dense cloud along and a few inches below the wide sloping eaves of one side of a byre, and similarly below the lintel of an open door on the same side. The low evening sun cast a shadow of the eaves and of the lintel so that the air space just below them was divided into an upper, shaded region and a lower, brightly illuminated one. The axis of the elongated cloud extended along this boundary, and the insects flew with an irregular flight, quite unlike the regular " dance " of swarming males and without any constant orientation, with the result that they kept close to the sunlight-shade interface.

The observation suggests visually controlled behaviour, not necessarily related to the more highly organised behaviour of the male swarms. There was no indication that the aggregation had any sexual significance. Hocking (1953 : 246) has described a possibly similar phenomenon in *Aedes punctor* (Kirby). Goetghebuer (1921 : 14) appears to suggest that females of several *Culicoides* species gather in clouds *before* attacking their human prey ; I feel, however, he is probably describing merely the obvious fact that when *Culicoides* (or other biting flies) are numerous there is a definite cloud of them, attracted by the host, constantly hovering near the host ; this somewhat obscure statement apart, there appears to be no similar record for any ceratopogonid.

C. pallidicornis Kieffer.—Many swarms of this species were observed in the woodland around Rossdhu Field Station, Dunbartonshire, on 1st July, 1947. Though varying in height above the ground from 1 ft. to 8 ft., all the swarms were very close to the top of the dense herbage and it seemed likely that the tips of bracken fronds were the usual markers. Observation of this small species was difficult, but the impression was that the insects were all facing in the same direction ; the flight consisted mainly of small side-to-side excursions with occasional spiralling movements upwards and downwards. The swarms consisted of a few to about 100 individuals and were subspherical and fairly compact. They were also extremely unstable, the males flying frequently in and out of the swarm so that many groups disintegrated and others formed ;

and at the same time there were many scattered individuals in the surrounding area not grouped in recognisable swarms. This instability was presumably caused by the extreme abundance of possible markers, so that from almost any position many other bracken fronds were visible.

Three samples contained 18 males, 15 males and 47 males, 1 female respectively, all of *C. pallidicornis*.

5. Other Ceratopogonidae.

Certain other Ceratopogonidae swarm in much the same manner as *Culicoides*, but some show interesting differences. Male swarms have been recorded in *Ceratopogon* spp., *Serromyia femorata* (Meigen) and *Palpomyia* spp. (Edwards, 1926) ; in *Atrichopogon* sp. and *Ceratopogon* sp. (Goetghebuer, 1921 : 14) ; and in *Leptoconops kerteszi* Kieffer (Freeborn and Zimmerman, 1934). Edwards (1920) described the females of *Palpomyia semifumosa* (Goetghebuer) (recorded as *P. brachialis* (Haliday)) flying in groups with the long dorsal abdominal glands everted ; evidently this is, in one aspect, outside the scope of this paper, but since Edwards at first mistook the group for a swarm of male chironomids it would seem that the flight pattern and its control may be related to those of the swarms described above. The observations made during the present work are detailed below.

Two swarms of males of *Stilobezzia ochracea* (Winnertz), each subspherical and consisting of about 30 individuals, were found in loose woodland at Rossdhu, Dunbartonshire, on 1st July, 1947, 18.00 hr. They were flying about 5 ft. above the ground in a small clearing among bracken. Small male swarms of *Dasyhelea* sp. were also seen at Rossdhu in very similar situations.

A species of *Atrichopogon*, however, has very different habits which strongly recall the second type of mating of *C. nubeculosus*. This is the species whose mouth parts were described by Gad (1951)—apparently *A. pavidus* (Winnertz) or a close relative. Both males and females settle in large numbers on the petals and adjacent parts of honeysuckle, primarily, it seems, to feed. The insects wander slowly and irregularly over the flowerheads, making no movements suggestive of distance recognition. When a male encounters a female he climbs over her from behind until the head is above the middle of the body of the female, and then curves his abdomen in a semicircle so that as the ventral surface of the hypopygium comes into contact with the female from below and behind the claspers can grip the terminal segments of the abdomen. Many pairs maintain this position throughout mating, but sometimes the male later loosens the hold with the legs on the dorsal surface of the thorax of the female, straightens the abdomen, and trails behind the female with his ventral surface uppermost. Less often, the abdomen of the male then becomes twisted through 180° so that he also is standing on the substrate, the pair of course facing in opposite directions. The hypopygium itself is, however, never inverted—even in the last-mentioned position the necessary twist in the abdomen is only a temporary one that takes place over a series of segments. Pairs remain *in copula* for a considerable time ; the two pairs so found separated after 30 and 75 minutes. The antennal setae of all males seen were decumbent. These

observations were made at Rossdhu, 3rd and 5th July, 1952 (mid afternoon and late evening).

A large swarm of males of *Probezzia* (*Dicrobezzia*) *venusta* (Meigen) was seen on the shingle beach of Loch Lomond at Rossdhu, initially at about 10 ft., but rising much higher when disturbed. At the time, 16.00 hr. on 27th June, 1949, there was bright sunshine and the swarm was probably above the edge of the shadow of trees on the shingle. Much later the same evening (20.00 to 21.00 hr.), females of *P. venusta* were watched in the same area hunting their prey; apparently the species shows the same sexual difference in time of activity that Parker (1949) demonstrated for *Culicoides pallidicornis*.

The beach of Loch Lomond where *P. venusta* was observed is fringed with alders to landward. Seen from below, the tips of the loose radiating branches with their complement of leaves stand out conspicuously against the sky. At 18.00 hr. on 27th June, 1949, small swarms of 3 to 20 insects were observed a few inches below the tips of many branches. Five swarms were sampled and all the specimens obtained were females of *Serromyia femorata*. The insects were obviously using the terminal twigs above them as swarm-markers, since they were always flying a few inches below the twigs and in no constant relation either to branches below them or to the ground. Thus in *S. femorata* both males (Edwards, 1926) and females are known to swarm, and in the swarms, at least at the moments when the various observations were made, the sexes are separate.

A swarm of *Ceratopogon* sp. also at Rossdhu, flying a few feet above a standing motor car, consisted of males and females in approximately equal numbers. In 1953, at Churchill, Manitoba, another swarm of *Ceratopogon* sp. was briefly studied. The swarm consisted of some thousands of individuals and was found in the lee of a spruce tree from 1 ft. to 7 ft. above ground. The forward individuals were within a few inches of the densely packed branches, but the swarm extended back over the low-growing vegetation for some 7 ft. to 8 ft. A general sweep through the swarm yielded males and females in approximately equal numbers; but a stroke of the net made immediately (6 in.) behind the branches gave a catch consisting of about 90 males and 10 females, whereas a stroke 6 ft. from the tree gave over 100 females. Thus the sexes, within a swarm appearing as one continuous whole, were evidently markedly segregated.

A large species of *Bezzia* ("*Bezzia* 2") observed at Churchill, Manitoba, in late July, 1951, provides another example of both sexes occurring together in the swarms. The swarms flew a few feet above boulders projecting from grassy tidal flats, at about 15.00 hr. (C.S.T.) on sunny days. A single sample consisted of 4 males and 3 females. (Plate II, fig. 2).

In late July, 1951, also at Churchill, Manitoba, a number of swarms of *Forcipomyia* (?) *cilipes* Coquillet were discovered flying above the tops of small spruces and larches. Several observed at 08.30 hr. on 27th July were flying immediately above the top of a tree (20 ft. to 25 ft. in height) in calm periods, but fell a few feet down the leeward side in winds of Force 1 (Plate II, fig. 1). A sample from one of these consisted of 90 males. A few days earlier, at about 16.00 hr., a similar swarm over a 10 ft. spruce yielded a sample of 29 males and 1 female. Other observations indicated that morning and evening swarming periods, at about the times mentioned, appeared to be the rule.

6. Discussion and Conclusions.

The above observations, incomplete though they are, lead to certain interesting conclusions and suggestions, and at the same time indicate other aspects of the sexual behaviour of *Culicoides* that are as yet obscure. Specifically, they yield a partial account of male swarming and throw some light on its cause and function ; and they also provide information about the mating process both as it occurs in flight in the swarm and also, in certain species at least, between non-flying individuals.

(a) *The Male Swarms.*

Swarming of males has been observed in eight species : *C. nubeculosus*, *C. riethi*, *C. pallidicornis*, *C. pulicaris*, *C. punctatus*, *C. delta*, *C. halophilus* and *C. grisescens*. Goetghebuer (1919, 1920) has observed it in Belgium in *C. pulicaris* and *C. fascipennis*. The phenomenon is evidently widespread and occurs in very diverse sections of the genus *Culicoides*, but with knowledge of its cause and function still incomplete it would be unwise to assume that it is exhibited by all species.

(b) *Swarming Site : Factors Determining Formation of Swarms.*

A swarm is typically stationary and has rather definite boundaries, though the insects themselves are in constant to-and-fro movement. Natural swarms of *C. nubeculosus*, *C. riethi*, *C. pallidicornis* and *C. halophilus* always occur more or less directly above a clearly defined object or area, the " swarm-marker ", that contrasts strongly in colour or brightness with the background. The markers used by swarms of any one of these species are closely similar and the type soon becomes recognisable, though from species to species there are obvious differences. All these points suggest that the position is determined visually. In *C. grisescens*, however, no marker was identified beneath the swarm ; nevertheless it is likely that the position was chosen by sight, since the swarm was equidistant from a number of conspicuous erect objects (trees). Possibly the difference between the two cases is that most species watch the swarm-marker with the ventrally directed ommatidia of the compound eyes, whereas *C. grisescens* uses the lateral elements. That different parts of the eye may be used by various species—or under various circumstances—is indicated by the observation that females of *Serromyia femorata* swarm high above the ground just *beneath* the tips of branches silhouetted against the sky. Again, under normal conditions *Forcipomyia ciliipes* watches the tops of spruce trees with the lower part of the eye, but in strong winds, when in danger of being swept backwards away from the marker, the insects drop down the leeward side of the tree and maintain position in relation to an object that is now in front of them.

If swarm formation is controlled by visible landmarks, it should be possible to cause swarms to develop at chosen places by presenting suitable objects. Many swarms of *C. nubeculosus*, *C. riethi*, *C. halophilus* and *C. punctatus* have in fact been induced artificially by presenting swarm-markers of cloth on natural or suitably prepared backgrounds. In the initial work on *C. nubeculosus* there was, however, some uncertainty about the stimulus involved, since the usual natural marker is a pad of cow-dung, which not only possesses a characteristic appearance but might also give off water vapour and other substances. Experi-

ments with dry, water-dampened and dung-impregnated cloths showed that all three were equally effective in producing swarms, and led to the conclusion that the significant stimulus was visual. Further, in a slight wind the swarm remained (at a height of several feet) directly above the marker, though chemical substances and convective heat given off by the marker would necessarily be carried downwind.

It might be supposed, nevertheless, that swarm formation depends on the gregarious habits of the midges themselves, and is independent of external influences. The decisive evidence to the contrary is that lone males were observed in flight over a marker, exhibiting, so far as could be determined, all the behaviour characteristic of the individuals of a fully developed swarm (*C. nubeculosus* at Chideock and at Airth ; *C. riethi*). It seems clear that the swarm is essentially a mere group of individuals that react independently to the one relatively local and rare external stimulus. Nevertheless it is possible (or even probable) that when a number of insects are over the marker simultaneously certain interactions between individuals occur ; and to that extent the swarm would become a functional unit. Such interactions are indeed suggested by the observation that when, as occasionally happens, swarms of *C. nubeculosus* and *C. delta* rise rather suddenly to an exceptional height, the swarm maintains its coherence throughout the movement. Even here, however, the apparent coherence might be due to precisely timed individual responses to, e.g., a sudden change in wind-speed. These apart, all observations on flight in swarms seem to be more readily explained in terms of the reactions of the individuals to the swarm-marker.

(c) *Factors Controlling Detailed Behaviour of Swarms.*

In the swarm all the individuals are oriented in the one direction and this orientation is always upwind. Experiments on *C. nubeculosus* made at the same place on successive nights, under diverse wind conditions, showed that the orientation was unrelated to surrounding objects (nearby hedges) or to the brightest (western) part of the sky, but always related to wind-direction ; and in *C. riethi* a swarm was watched adjusting its orientation to the veering wind. Flight in the swarm consists of short forward-and-backward, side-to-side and vertical excursions, but as already emphasised the insects face upwind in all phases. The factors controlling the extent of the vertical excursions are unknown. The extent of the side-to-side movements is probably regulated by the lateral margins of the marker, since with a rectangular marker in the line of the wind the swarm flies equidistant from the two sides (*C. riethi*). The forward-and-backward movements may be controlled similarly by the upwind and downwind margins, but the evidence here is confused. Some swarms flew over the downwind margin rather than directly above the marker, as in the instance where *C. riethi* was watched flying upwind into the swarm and starting the evolutions over the first-encountered margin. It is likely that phototactic responses play some part in determining swarm position and are involved in the apparent discrepancy between the behaviour of *C. nubeculosus* at Airth, where some swarms appeared to be determined by dark-coloured markers and others by light ones, and at Chideock, where dark markers only were used ; but until fuller observations are available this matter also must remain obscure.

Over and above these detailed aspects of the swarming " dance "—which

are perhaps necessary aerodynamically—there remain the stationary position of the swarm over the marker and the constant upwind orientation of all individuals. Kennedy (1939) made a laboratory study of the behaviour of unfed females of *Aëdes aegypti* (L.), and concluded that in addition to phototactic responses there is also a response to the movement, as such, of the object seen. If mosquitoes were flying in a cage with a pattern of parallel stripes on the floor, and the stripes were slowly drawn forward, the insects oriented themselves to face in the direction of movement and flew forward with the stripes, or rather, they flew forward with the stripes at a speed slightly exceeding stripe-speed so as to make a limited progress with respect to the background. Similarly, if the stripes remained stationary but a wind was caused to blow through the cage, the insects again oriented themselves against the wind and flew forward so as to make the same limited progress over the background pattern (the *ground-speed* of the mosquitoes being evidently lower than in the first experiment when the stripes were moving). Kennedy points out that the two cases are visually identical ; in the one the air is still and the background moving forward, and in the other the background is still and the insects tend to be carried backwards in the moving air ; in each they orient themselves and fly so as to avoid all movement from back to front of the ground pattern over the eyes, and so as to achieve a certain moderate front-to-back " retinal velocity ". He further points out that it is impossible for a flying insect to orient itself in relation to the wind directly ; it can do this only through visual inspection of the apparent direction of movement of the landscape, since mechanically it is at rest when being carried downwind at wind-speed and in this state can fly equally well (in the absence of visual control) in any direction. It is obvious that the behaviour of *Culicoides* swarms presents close parallels with these observations. The midges are oriented upwind because they are visually attached to the marker, which, except for this compensatory upwind flight, would appear to be receding forwards. Over all, the midges fly with an air-speed that is just sufficient to prevent this back-to-front movement on the eyes, without, however, setting up the moderate front-to-back movement preferred by the mosquitoes, i.e., the swarm remains stationary above the marker ; yet if the whole swarming dance is considered it is seen that the midges are making short flights in which a front-to-back movement is achieved, alternating with brief phases in which they allow themselves to be carried backwards on the wind. Thus movement-vision seems to be all-important in determining the existence and position of swarms, while phototactic and probably also other types of responses also operate and perhaps determine the character of the markers used by the various species.

If the wind rises, the swarm of *C. riethi* flies at a lower height, where presumably friction with the ground reduces the wind-speed ; finally, at winds of about 2 m.p.h. the insects settle on the marker. Similarly Kennedy's *Aëdes aegypti* settled as the wind rose rather than permit the back-to-front movement they were otherwise unable to prevent. In general, the swarms of *C. nubeculosus* remained with remarkable constancy directly above the marker, indicating an accurate adjustment of air-speed of flight to the prevailing conditions—again similar to *A. aegypti* which adjusted its air-speed as the wind increased so as to make the same moderate progress over the background

pattern up to the limiting wind-speed at which it settled—but occasionally they were carried backwards a few feet behind the marker, possibly when a sudden gust came too rapidly for the swarm to fall to a region of lower wind. In *C. nubeculosus* also all flight had ceased at winds estimated at 2 to 3 m.p.h. Presumably this is the maximum air-speed that *C. nubeculosus* and *C. riethi* are capable of, and therefore in still air their rate of free (non-swarming) flight would never be higher; possibly this is a partial explanation of the very limited total range of flight from breeding centres (Downes, 1950), a limitation that applies not only to *C. nubeculosus* but also to *C. impunctatus*, as Kettle (1951) has amply demonstrated, and probably to many other species.

The observations that the swarms of *C. nubeculosus* and *C. halophilus* fly at a greater height over large markers than over small ones are also agreeable to the hypothesis of visually-controlled flight, since a large marker seen from greater height has the same apparent size as a small one seen from a lesser. Similarly, species that are adapted to use markers that are in fact small (*C. pallidicornis* and *C. halophilus*) characteristically swarm at much lower heights than others. (The instability of swarms of *C. pallidicornis* as contrasted with those of *C. halophilus* apparently depends on the fact that the bracken frond markers used by the former are plentiful and many are visible at one time, whereas *C. halophilus* from its swarming position cannot see other possible markers.) It is to be noted that swarms evidently do not usually fly at the lowest possible height—*C. riethi* flies lower than normal when the wind rises; nor at the greatest possible height (the height at which an object of the size of the marker can just be resolved)—swarms of *C. nubeculosus* occasionally rise much higher than usual, retain their coherence and descend again, still above the marker, to normal height. It is evident that the question of the regulation of the characteristic height of flight is in need of investigation.

(d) *Monospecific Swarms.*

Throughout this study no "mixed" swarms, consisting of more than one species, were observed. Yet in all the areas where observations were made there were many species of *Culicoides* in the adult stage—at Chideock and Airth about ten, at Rossdhu seven, and so on. At several sites very closely related species were available—*nubeculosus* and *riethi* at Airth and two or more members of the *pulicaris* complex at Airth, Bannachra Moor and Glasgow University. Indeed these monospecific swarms have recently been cited by Downes and Kettle (1952) as confirming the distinctness of the closely-related species of the *C. pulicaris* group. The phenomenon seems to depend principally on the specificity of the swarm-markers, as already mentioned, together with specificity in height of flight, other factors being equal, over a given marker. Thus on one occasion *C. riethi* and *C. punctatus* were swarming simultaneously at different heights over the same marker; on another occasion there were three swarms, two of undetermined chironomids and the other of *C. riethi*. Other factors probably involved include specificity in the area of flight (even when two species occur in, say, the same field) and in time of flight, a point that was not adequately investigated in these studies but one that was amply demonstrated for *Culicoides* spp. by Parker (1949). Reports of "mixed swarms" in other Nematocera, e.g., swarms composed of various species of mosquitoes (Marshall, 1938), one of *Pelopia falcigera* Kieffer (Tipulidae) and *Culicoides*

pulicaris and another of no less than eight species of chironomids (Goetghebuer, 1921 : 13), perhaps depend upon a misconception arising from a rather closer than usual approximation in the behaviour of species using the same marker. If the swarms are the usual mating-sites, this specificity of swarming habits may be an important mechansim of the reproductive isolation of closely related forms.

(e) *Entry of the Female into the Swarm : Mating.*

The occurrence of mating within the swarm was demonstrated in only two species (*C. nubeculosus* and *C. riethi*) and on very few occasions. Few as they are, these records should not be discounted ; observation of these very small insects is difficult and demands a well-sited swarm that can be watched for long periods against a background of clear sky—conditions that are virtually unobtainable for low-flying species such as *C. pallidicornis* and *C. halophilus*. It was shown that *C. impunctatus* and *C. obsoletus* also certainly mate in flight, and probably while swarming.

In *Culicoides* the swarm is always basically of males although in several species individual females were found in the samples. Whether the female flies into the swarm by chance—in which case swarming would have, at the best, no special reproductive value since chance encounters with males could not be more likely than when the latter were dispersed—or by a specific pattern of behaviour on the part of the female that would result in concentrations of the two sexes at definite restricted places, is, strictly speaking, unknown. There is, however, some evidence that the latter is the case. The position taken up by the cloud of female *C. obsoletus* suggests strongly that this sex also controls its flight by visual means. Furthermore, in the related genera *Serromyia*, *Bezzia* and *Ceratopogon* the females themselves carry out a typical swarming flight controlled by a marker. In *Spaniotoma minima* (Meigen) (Chironomidae) Gibson (1942) has shown that both males and females participate in the swarm, apparently over a marker, but males soon predominate since as pairs form they fall to the ground and the females do not rejoin the swarm on the completion of mating. All these observations suggest that the females of *Culicoides* can perceive and react to objects of the kind that males use as swarm-markers ; perhaps females also are attracted to such objects, possibly even to the specific male swarm-marker. If this suggestion is correct, it is clear that in *Culicoides*, which has a 1 : 1 sex-ratio on emergence (see the rearing records of Cameron, 1948, and Kettle and Lawson, 1952), pairing must take place almost immediately on the entry of the female into the swarm. In *Ceratopogon* sp., on the other hand, the females, which certainly swarm in relation to the same object as that used by the males, appear to delay their entry into the " male zone " of the swarm and thus spend a considerable time in flight before mating. With regard to the suggestion that the females of *Culicoides* also may respond to the specific male swarm-marker, it may be recalled that in all seven matings here recorded the male was in fact paired with a female of his own species though many other species were flying at the same time. If we conclude that this is indeed the case, swarming is evidently of great value in reproduction, since dispersed individuals of both sexes are drawn to and held at a limited number of very small areas, thus ensuring the opportunity of mating.

It was shown repeatedly that during swarming the males hold the long setae

of the antennae in the "erect" position, at an angle of about 70° from the shaft. Long antennal setae of this type are found in the males of many other Nematocera, and their function has been investigated by several workers, most recently by Roth (1948) in *Aëdes aegypti*. He showed that when the setae are erect the antenna is set into vibration by sound waves of a frequency around that emitted by the female in flight. The efficient range of frequencies was, however, fairly considerable so that a specific response to the exact frequency of the female of a particular species seems to be out of the question; indeed the frequency changes with the age of the insect. This vibration of the shaft stimulates the battery of organs of the chordotonal type in the pedicel, and thus the antenna functions as an auditory organ. If the setae are decumbent, as they are in *A. aegypti* during the first day or two of adult life, or if they are artificially removed, much more energy is needed to produce movement of the shaft, and practically speaking the organ is non-functional. Males with erect hairs orient themselves towards the source of the sound and show grasping and clasping responses; in the natural situation therefore they pounce on and mate with a female flying nearby.

It seems evident that the same processes occur in *Culicoides*, since males flying in the swarm with erect antennal hairs seize and mate with females flying into it. There is no reason to suppose that the males can perceive the female by sound until she is within the swarm—the energy level of the sound is too low, nor did Roth demonstrate any but a short-range effect in *A. aegypti*—or that the recognition by sound is specific—the range of frequencies eliciting the mating response, in *A. aegypti* at least, is too great. Nor is it likely that the females are attracted to the swarm by sounds emitted by the male—the hairs of the female antenna are short and presumably cannot assist the shaft to vibrate and the chordotonal apparatus of the pedicel is relatively ill-developed. The arrival of the female, and of the appropriate female, more probably depends on a visual response by the female to the specific male swarm-marker, after which she is located auditorily by the process described by Roth.

Once the antennal setae of *A. aegypti* are erected, on the second day of adult life, they remain so; the insect is therefore always ready to mate with a flying female. In all species of *Culicoides*, however, the normal position of the setae of a captive insect is decumbent and the males with erect setae taken from a swarm rapidly fold them. Readiness for mating must therefore be a more temporary state, dependent on appropriate conditions. The stimulus leading to erection is unknown: *C. riethi* and *C. halophilus* at least occasionally erect the setae in captivity (without flight), but *C. nubeculosus* apparently does not. Whether erection precedes flight as such, or sets in only over a swarm-marker, is also unknown; possibly free-flying males also have erect antennal hairs and are ready to mate with chance-encountered females. It should be noted that, except for the possibility that the antennal setae are erected only under the stimulus of the swarm-marker, there is no evidence that the aggregation of males in the swarm is itself stimulatory and leads to a state of readiness for mating, as has been suggested by Gibson (1945) and certain other authors.

Mating in flight appears to take place rapidly and efficiently; the mating lasts only a few minutes and the female remains quiescent until a few moments before the pair separate.

(f) *Mating without Flight.*

C. nubeculosus can mate not only while in flight in the swarm, but also by an entirely different sensory process while both the male and female are at rest. The female is not emitting sound, since the wings are folded, and the male is not auditorily receptive, since the antennal hairs are decumbent. Recognition of the female takes place only on extensive contact, probably mediated by tactile or contact chemoreceptor organs ; the recognition is non-specific, that is, the male reacts not only to the appropriate female but also to other males and to females of other species ; clasping movements are active but inaccurate and copulation is often not achieved. Nevertheless, such matings are frequent in captivity and lead to impregnation. On rare occasions the same behaviour is shown by *C. riethi*, but it has not been noticed in any of the many other British species of *Culicoides* handled or, except in one species of *Atrichopogon*, in a number of other genera.

Pomerantzev (1932) has described mating without flight in *C. nubeculosus* in the Novgorod area of Russia. A translation of his interesting account may be of value : " If the cows have to stand in the open for a long time, the surface of their bellies begins literally to swarm with these lively insects [*Culicoides* spp.], and one can only be astonished at the nimbleness and speed with which these minute creatures get about in the animals' hair. Most of the individuals attacking the cows are females, although in May they are joined by a considerable percentage of males [of *C. nubeculosus*]. Copulation proceeds as follows : the female, sucking blood, is usually completely submerged in the cow's hair, and only in places very sparsely covered with hair can the tip of the insect's abdomen be seen projecting almost perpendicularly to the surface of the cow's hide. Having found a female the male quickly grasps the tip of her abdomen with his forceps, holding on to the surrounding hair of the animal with his legs. Meanwhile the female remains in her previous position and the pair does not alter its position until the female is replete with blood. Having become so, she climbs out on to the surface of the hair covering, after which the pair crawls up and down for a while until some reason or other causes it to leave the animal. It is difficult to judge from the few cases observed how long copulation continues. Pairs placed in a test tube remained *in copula*, in some instances, for about an hour."

It cannot be regarded as certain that the insect that Pomerantzev names *Culicoides nubeculosus* and the one to which the same name is attached in Britain are identical, but the figures of the Russian form make it clear that the two are at least very closely related. It is probably valid, therefore, to discuss the two groups of observations together. On this assumption, it is seen that his account agrees completely in the main point that mating can take place without flight, though it differs from the laboratory observations in various details, e.g., the longer duration of copulation. It also suggests that mating under these natural conditions is more efficient than in captivity, and indicates clearly that preceding the discovery of the female there is another behaviour pattern, only hinted at in the present work, viz., the landing of the males on the host of the female (cows), which tends to bring them into close proximity with the non-flying females. It seems therefore that again there are two stages in the process of mate-finding, comparable to the visually controlled assembly at the swarm-markers followed by short-range auditory recognition as suggested for mating in flight. Possibly the parallel may be even closer, since it may well be that

settling on the host is the more specific action (as was suggested for assembly at the swarm-markers); certainly the second stage, the tactile recognition, is non-specific under laboratory conditions and cannot by itself ensure the appropriate mating.

In the terminology of mosquito specialists, therefore, *C. nubeculosus* can behave both as a stenogamous and as a eurygamous species. However, as Bates (1949: 51–52) indicates, the term stenogamous has a certain lack of precision, and as originally introduced and customarily used it signifies merely that the mosquito concerned can mate in " small " cages and does not need large insectaries or open fields. It is often not stated whether flight or swarming takes place in these " small " cages or whether males mate with resting females. For *C. nubeculosus* it has been clearly shown that there are two radically different processes of mating, the one taking place at rest, the other depending on flight, and not merely an ability to fly in comparatively small enclosures.

In conclusion, a brief note on the mating posture may be added. On emergence from the pupa the hypopygium of the male of *C. nubeculosus* is, as in all Nematocera, in the anatomically normal position, with the terga dorsal and the sterna ventral. During mating (of either type) the ventral surface of the hypopygium, i.e., the aedeagus, is applied to the ventrally placed female opening from behind, i.e., with the claspers pointing towards the head of the female, as shown by Pomerantzev, 1932, figs. 23 and 24. The normal mating position (not always fully achieved in stenogamic matings) is, however, for both male and female to stand on the substrate facing in opposite directions. Clearly therefore the terminal segments of the male are inverted (180° twist) with respect to the anterior part of the body.

The hypopygium rotates to a considerable extent during the first day or two of adult life, the twist occurring between the seventh and eighth and between the eighth and ninth segments. Torsion may be either left- or right-handed (as noted also by Tokunaga, 1937). Completion of the rotation to 180° is achieved only on mating and is perhaps the mechanical result of the normal stance.

Though other species of *Culicoides* often exhibit slightly tilted hypopygia, the distinct rotation that occurs in *C. nubeculosus* is unusual (Tokunaga, 1937; also personal observation). Inverted hypogyia are, however, found in certain other genera of the family (Edwards, 1926). *C. nubeculosus* also appears to differ from other Nematocera that exhibit torsion in that the twist occurs between segments seven and eight and between segments eight and nine, instead of entirely between segments eight and nine, and that torsion may be in either direction, instead of always clockwise (see van Emden, 1953).

The behaviour of *Atrichopogon pavidus* resembles that of *C. nubeculosus* rather closely. Mating takes place at rest, with no distance recognition, and with antennal setae decumbent. The males reach the general location of the females by landing on the flowers on which the latter are feeding. In this case the males obtain food (nectar) from the same source, so that landing on the flowers may not have the same direct relationship to mating as does the remarkable landing on cows by the males of *C. nubeculosus*. The posture of the male during mating also differs from that of *C. nubeculosus* in that the more usual posture does not require the inversion of the terminal segments, and even in those cases in which both male and female are standing facing away from one another, the inversion is brought about by a general twist of the abdomen, not by an inversion of the hypopygium as such.

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8. Summary.

1. Swarms, usually almost entirely of males, occur in many species of *Culicoides* and in other Ceratopogonidae.

2. The swarms are always related to a distinct object, the swarm-marker. Observation and experiment showed that the swarm-marker is recognised visually. Each individual responds to the marker independently ; the swarm therefore is not primarily an example of gregarious behaviour.

3. Movement-vision is involved in the response to the marker, since in all phases of the swarming flight the insects are oriented upwind. Phototactic responses may play some part in determining the precise relationship of swarm to marker.

4. Swarms vary in behaviour in response to wind-strength, size of marker, abundance of markers, etc. ; all these phenomena are readily explained by the visual theory.

5. No swarms consisting of more than one species were found, and there is evidence that the swarm-markers are specific.

6. In *Culicoides* individual females are often found in a basically male swarm ; in several species of other genera males and females fly in relation to the same marker. It is suggested that females of *Culicoides* respond to the male swarm-marker and fly into the swarm, but mate very rapidly after entry. Mating pairs have been observed forming within the swarm.

7. It is probable, therefore, that swarming is useful as a means of bringing dispersed males and females into close proximity, and also, if the markers are specific, that it functions as an isolating mechanism.

8. Within the swarm, mating is brought about by an auditory recognition of the flying female by the male ; the latter always swarms with the antennal setae in the erect (auditorily receptive) condition. It is likely that this recognition is non-specific.

9. *C. nubeculosus* and *C. riethi*, but not other species, are able to mate by a second process while at rest (i.e., not involving sound-production and audition). Recognition at chance encounters depends on contact. It is non-specific, at least under laboratory conditions, and sexual recognitions of males and of females of other species are described. In *C. nubeculosus* it is said to be preceded by behaviour (settling on the female host) that brings the male into close proximity to the female ; this phase might be specific. *Atrichopogon pavidus* shows comparable behaviour.

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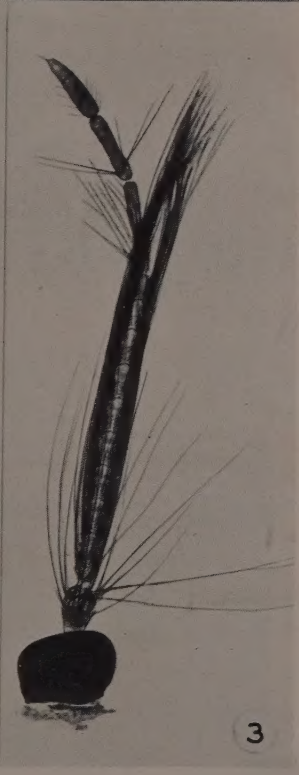
PLATE I.

Culicoides nubeculosus Meigen.

Fig. 1.—Natural and experimental swarm-markers, Chideock, Dorset. The four markers are, in order, a wet muddy area, a fresh pad of cow-dung, two dry dark cloths.

Fig. 2.—Antenna of male with setae erect.

Fig. 3.—Antenna of male with setae decumbent.



The swarming flight and mating of *Culicoides*.

J. A. Downes.

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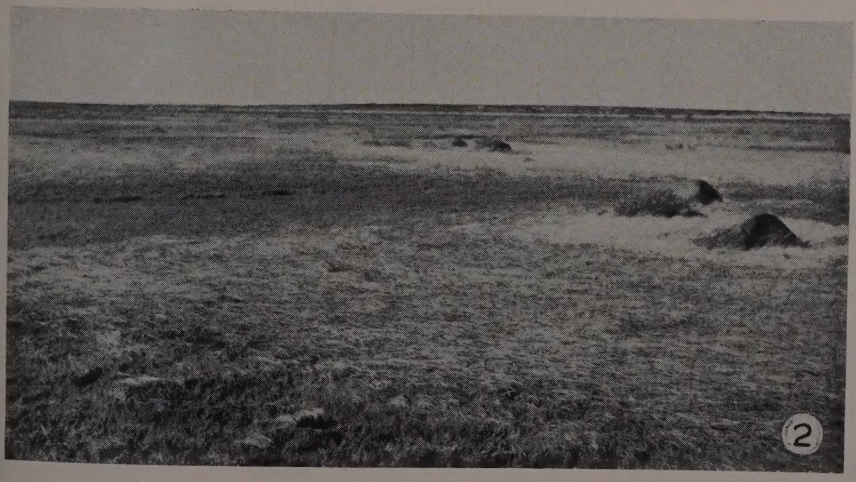
PLATE II.

FIG. 1.—*Forcipomyia* (?) *cilipes*. Male swarm flying above top of a 25-ft. spruce tree, wind-speed virtually nil. Churchill, Manitoba.

FIG. 2.—*Bezzia* sp. Swarm-markers (ice-borne boulders on tidal flat). Churchill, Manitoba.



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